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The pollination ecology of *Viola*. 2, Pollen loads of insect-visitors

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ABSTRACT

The pollen loads of insects associated with populations of *Viola riviniana* Reichb., *V. reichenbachiana* Jord. and *V. hirta* L. were analysed. An unexpected variety of insects carried *Viola* pollen either alone or mixed with foreign types. Combinations of more than two types (when one was *Viola*) were rare among the pollen loads of bees but common among those of hoverflies. Despite the deliberate selection for study of areas with high densities of *Viola* flowers there appeared to be some assortative foraging among the *Viola* visitor-species: the solitary bees and hoverflies exhibited preferences for actinomorphic flowers, while the social bees exhibited preferences for stereomorphic and zygomorphic flowers. However, by flowering very early in spring, *Viola* may experience little competition for pollen vectors and, by harbouring both nectar and pollen, the chasmogamous flowers may provide vital food sources for anthophilous insects and so receive frequent visits. This may contribute significantly to the incidence of cross-pollination.

Many insects which carried pure loads of *Viola* pollen had foraged exclusively among its flowers and shown temporary constant behaviour toward them. Such constancy exhibited by a variety of visitor-species would have two important effects upon pollination: firstly, the quantity of compatible pollen transferred to the stigmatic cavities would increase, thereby ensuring the maximum fertilization of ovules. Secondly, pollen exchange between chasmogamous flowers would be maintained, possibly at a significant level for the immediate and future evolution of the population.

INTRODUCTION

Many species of *Viola* produce seed by means of both cleistogamous and chasmogamous flowers. The cleistogamous flowers are cryptic, obligately self-pollinated and yield the majority of seed in any given season (Valentine 1962, Clausen, Channel & Uzi Nur 1964). By contrast, the chasmogamous flowers are conspicuous, dependent upon insect visits for pollination and frequently fail to set seed. For this reason, in-breeding seems to be the rule with occasional out-breeding resulting from irregular visits of insect pollinators to the chasmogamous flowers. As an insect visit may initiate a small burst of variation through cross-pollination, it may be of considerable importance to the evolution of the population involved. Unfortunately, because of the irregularity or rarity of insect visits, they are extremely difficult to sample. One means of circumventing this problem is to collect insects associated with the chasmogamous flowers and to examine their pollen loads for *Viola* pollen. Its presence betrays a visit to a violet flower. In this way a large enough sample may establish the frequency of visits and consequently the possibilities for out-breeding. The additional value of pollen load analysis is the evidence provided on the foraging

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patterns of pollen vectors. These, in turn, reflect some of the ecological factors operating on the in-breeding/out-breeding balance in *Viola* populations.

MATERIALS AND METHODS

The selection of habitats was governed by the location of suitably sized populations of one or more of the species *Viola riviniana* Reichb., *V. reichenbachiana* Jord. and *V. hirta* L. All the habitats chosen were in the chalk countryside of southern England, six near Winterslow, Wiltshire and one near Mickleham in Surrey. These have already been described in detail (Beattie 1969).

Collections of insects were made during the spring months of 1966 and 1967. Each day was divided into two collection periods, 10.00–13.00 hours and 14.00–17.00 hours, during which insects actually on violet flowers, and airborne insects in the habitat, were trapped and preserved. Forty-three species were found to have visited *Viola* flowers and these were termed visitor-species. Four hundred and one specimens of these were captured for examination, many whilst actually feeding from the flowers. Two hundred and fifty specimens of what turned out to be non-visitor-species were also trapped and examined. These included Lepidoptera, Diptera, Coleoptera, Hemiptera, Araneida and Opiliones.

Immediately after capture each specimen was placed in a 4:1 mixture of 70% ethanol and glycerol in an individual vial. The glycerol formed a viscous layer around the specimen which maintained integumental pollen at its original location. The term ‘pollen load’ commonly refers to the pollen accumulated by the specialised collecting hairs of bees (the pollen baskets). In the present study it was used to denote all the pollen carried by an insect including that found in the alimentary canal. Therefore, two operations were required for the analysis of each load: firstly, the examination of the integument and the centrifugation of the preservative (to concentrate any dislodged grains) and secondly, the scrutiny of the gut contents and faecal material.

Pollen preparations were mounted in fuchsin glycerine jelly. This semi-permanent mountant stained the grains red and rendered them instantly conspicuous among extraneous material.

A NOTE ON POLLEN CLASSIFICATION

A series of standard pollen preparations of species flowering in the habitats facilitated the identification of pollen removed from insects. Material was collected at the time of study and herbarium material was used as little as possible.

Pollen grains from 14 plant species were identified from the pollen loads. The flowers of these species were classified according to Leppik (1957). This scheme, which used characters of the form and symmetry of the flowers, was suitable for the detection of tendencies amongst the visitor-species to confine foraging to flowers of a particular structure or colour. In Leppik’s classification, flowers may be actinomorphic, pleomorphic, stereomorphic or zygomorphic. Actinomorphic flowers are characterised by radial symmetry; the floral organs are arranged on one level, hence pollen and nectar are not usually concealed. Pleomorphic flowers are similar to the last but possess a smaller number of petals; 3, 5, or 6 are common. In stereomorphic flowers the nectar is concealed and insect-visitors must be able to distinguish three-dimensional patterns in order to locate it. Zygomorphic flowers are similar to the last but are characterised by bilateral symmetry.

Three species were difficult to fit into the scheme and were designated according to the availability of their nectar and pollen. The flowers of *Endymion non-scriptus* were regarded as stereomorphic because the corolla partially conceals the pollen and nectar and insects must probe deeply to find it. The category of actinomorphic flowers was expanded to include the actinomorphic inflorescences of *Taraxacum officinale* and *Bellis perennis*. This was done because the attraction mechanisms of these particular flowers and inflorescences were very similar: firstly with regard to the outlines, colours and colour contrasts, and secondly, food was as accessible in the inflorescences as in the flowers. In the flowers nectar was not concealed and in *Taraxacum* it usually filled the corolla-tubes nearly to the top. The pollen of both *Bellis* and *Taraxacum* was liberally dusted over insects which merely crawled over the capitula and was, therefore, as accessible as the pollen of actinomorphic flowers. In both types pollen and nectar were readily available to short-tongued insects.

A NOTE ON THE INSECT VISITORS

A full account of the insect-visitors of *Viola* is to be published shortly but a few comments are necessary here. The list of 43 visitor-species comprised 2 species of Lepidoptera, 21 species of Hymenoptera and 20 species of Diptera. The number and variety of insects in this list contrasted sharply with the paucity and uniformity of species in the lists of other authors (Saunders 1846, Muller 1883, Knuth 1908, Veerman & Van Zon 1965).

Two dimensions of insect-visitors generally considered to be important in the pollination of many flowers including violets, are the length of the extended proboscis and the total length (Knuth 1908). These are considered important in the pollination of *Viola* flowers because they partially determine the details of feeding behaviour, for example whether pollen or nectar can be taken, and in turn the extent of the contact between the insect and the floral genitalia.

All the visitor-species fell into four discrete categories according to the length of the proboscis:

1·0 – 4·0mm	Small solitary bees (*Halictus*), small hoverflies (*Platychirus*) and all the casual visitors.
5·0 – 7·0mm	Large solitary bees (*Osmia*), large hoverflies (*Rhingia*, *Eristalis*) and honeybees (*Apis*).
9·0 –10·0mm	Bee-flies (*Bombylius*), short-tongued bumblebees (e.g. *Bombus terrestris* L.).
13·0 –14·0mm	Longer-tongued bumblebees (e.g. *Bombus hortorum* L.).

Most of the visitor-species fell into two categories according to total length (which did not include the extended proboscis, antennae or sting):

6·0 –11·0mm	Most solitary bees, all hoverflies, bee-flies, and all scavenger flies.
16·0 –18·0mm	Most bumblebees, cuckoo bees.

At the extremes there were two further categories:

3·0 – 5·0mm	Very small species of solitary bee.
19·0 – 21·0mm	Large bumblebee species.

Three species of fly, *Bibio johannis* L., *Orthellia cornicina* Fabr., and *Scopeuma stercorarium* L., were very common in the habitats but were only occasionally observed visiting violet flowers. Adults of *Bibio* and *Scopeuma* were known to be predacious on other insects (Colyer & Hammond 1951, Hobby 1933, 1934), and those of *Orthellia* were known to be coprophilous and necrophilous (Colyer & Hammond 1951). For these reasons it was thought that these insects were unlikely to visit violet flowers frequently and were probably of little significance as vectors of *Viola* pollen. Examination of large collections of them revealed that only 5% carried any pollen at all; consequently they were termed 'casual visitors'.

RESULTS

FORAGING

All the insects examined fell into one of the following four groups: 1. those which carried only *Viola* pollen, 2. those which carried a mixture of *Viola* pollen and foreign pollen, 3. those which carried only foreign pollen, and 4. those which carried no pollen at all. Fifty-five combinations of the fourteen pollen species were found in the pollen loads. These species were: A. from actinomorphic inflorescences: *Taraxacum officinale* agg., *Bellis perennis* L. (*Salix* spp. were included in this class), B. from pleomorphic flowers: *Ranunculus ficaria* L., *Anemone nemorosa* L., *Fragaria vesca* L., *Prunus spinosa* L., (*Fagus sylvatica* L. and *Mercurialis perennis* L. were included in this class), C. from stereomorphic flowers: *Endymion non-scriptus* (L.) Garcke, *Primula vulgaris* Huds., D. from zygomorphic flowers: *Viola* spp., *Ajuga reptans* L. and *Glechoma hederacea* L. This list reveals that anthophilous insects were exploiting almost every kind of flower available in the habitats.

Table 1 presents the evidence on foraging derived from the content of pollen loads. Of the 401 specimens examined, 144 individuals carried *Viola* pollen, 46 (32%) as completely pure loads and 98 (68%) as a mixture of *Viola* and foreign pollen. Sixty loads containing the most frequent pollen species are listed in column 4. The remaining 38 combinations were so infrequent as to provide little significant information on foraging save that occasional visits were made to less frequent flowering species.

Forty-six individuals representing all four visitor classes carried completely pure loads of *Viola* pollen (column 3), while an additional 19 carried a pure load of *Viola* pollen either on the integument or in the gut with different pollen at the alternative site (column 4, V). Solitary bees carried the largest number of pure loads of both *Viola* and of foreign pollen. Seventy-two per cent of the specimens examined carried pure loads of one genus, 50% being pure loads of *Viola*. Most individuals of *Osmia bicolor* Schrank carried a pure load of *Viola* pollen, while a smaller proportion of *Andrena* spp. and *Halictus* spp. did so too. Social bees came second to solitary bees with regard to numbers of pure loads. Sixty-nine per cent of these insects carried them, 46% being *Viola* alone and the rest being chiefly *Endymion* and *Primula*.

Key to pollen species

V	*Viola* spp.	E	*Endymion non-scriptus* (L.) Garcke
T	*Taraxacum officinale* agg.	A	*Ajuga reptans* L.
B	*Bellis perennis* L.	M	*Mercurialis perennis* L.
P	*Primula vulgaris* Huds.		

Mixtures of *Viola* plus one of three other pollen species not shown accounted for a further 38 records, but each one occurred so rarely that inclusion was not warranted.

TABLE 1. ANALYSIS OF THE COMMONEST TYPES OF POLLEN LOADS OF *VIOLA* VISITOR-SPECIES

	2		3	4												
Insect Group	Species	Number of specimens examined	Number of specimens which carried *Viola* pollen and no other type	Number of specimens which carried pure pollen loads or a mixture with *Viola* at one or both of the two sites (integument and gut) †												
				V	E	E+V	T	T+V	M	M+V	P	P+V	A	A+V	B	B+V
SOCIAL BEES	*Apis mellifera*	4			1											
	Bombus spp.	22	10	12	2						3					
	Totals:	26	10	12	3	10		2			3	1		1		1
SOLITARY BEES	*Osmia bicolor*	17	11	18												
	Andrena spp.	24	6	6			2						1			
	Halictus spp.	13	3	3			9									
	Totals:	54	20	27			11	6		1			1	4		3
HOVER-FLIES	*Rhingia campestris*	20	5	5	3		1		2							
	Eristalis spp.	15	3	3	1		1		1							
	Platychirus spp. & *Melanostoma* spp.	81	4	10	15		3		9		1				3	
	Totals:	156	12	18	19	8	5	4	12	7	1	1		1	3	2
FLIES	*Bombylius major*	20	1	5							16					
	Casual visitors	43	3	3	2		1		6						1	
	Totals:	63	4	8	2	1	1	2	6	1	16	4			1	
	Totals:	299	46	65	24	19	17	14	18	9	20	6	1	6	4	6

† If the particular load is restricted to one site, other pollen types may be present at the alternative site. Column 4V, for example, will include specimens with only *Viola* pollen (Column 3) and any specimens with *Viola* pollen at one site and another pollen type at the other.

Forty-seven per cent of hoverflies carried pure loads, 15% being of *Viola* only and the rest chiefly *Taraxacum*, *Bellis* and *Mercurialis*. The fly group included the bee-fly *Bombylius*, which contributed most of the scores for pure pollen loads in this category, excepting *Viola*, which was found chiefly on scavenger flies.

Two hundred and fifty-seven individuals carried either foreign pollen only or none at all. Of these, 138 were the casual visitors. It is possible that in some habitats the abundance of these insects may compensate for the rarity of *Viola* pollen in their pollen loads and so contribute to pollen exchange. However, as mentioned in the previous sections, this did not appear to be the case in the habitats studied.

Fig. 1 presents a record of foraging according to the numbers of plant species visited. Solitary bees were most constant to *Viola* and, in common with the social bees, rarely visited more than two species on individual foraging trips. All four groups showed some constancy to *Viola*, but the hoverflies exhibited the most indiscriminate foraging.

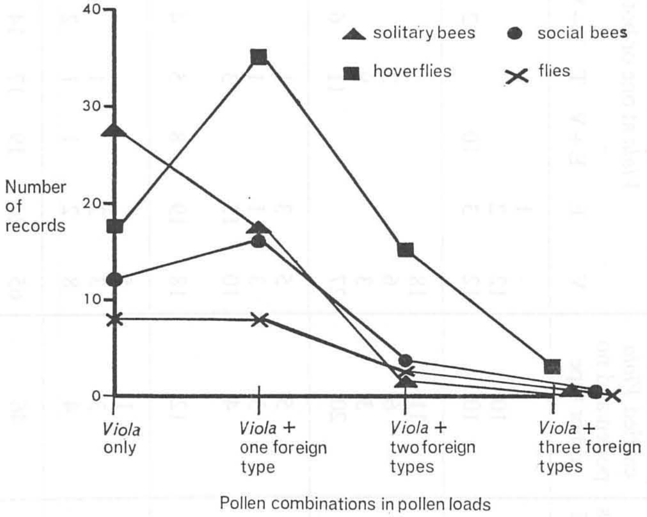

FIGURE 1. The number of pollen species in the pollen loads of the four groups of *Viola* visitors.

In Fig. 2, the foraging insects are grouped according to the floral structure of the species visited with a view to determining what importance this may have had on visiting behaviour in habitats apparently dominated by *Viola*. The first clear result was that actinomorphic and pleomorphic flowers were as important as violet flowers. Where *Viola* pollen was found in mixed loads, it was most frequently associated with actinomorph/pleomorph pollen. Inspection of Table 1 shows that this was chiefly a result of the loads carried by hoverflies and scavenger flies, and to a lesser extent solitary bees. Pollen loads of hoverflies exhibited the greatest complexity, including one load containing 5 pollen species. These 5 species represented a great variety of floral structure and enhanced the hoverfly reputation for the most promiscuous foraging. By contrast, the loads of social and solitary bees indicated a preference for stereomorphic and zygomorphic flowers: the commonest pollen combination for bumblebees was *Viola* plus *Endymion*, and *Viola* plus *Ajuga* was an important combination for solitary bees. Overall, the pollen most commonly associated with *Viola* was *Endymion* (Table 1, column 4). Individuals of each of the four visitor classes carried loads of foreign pollen but this was especially true of hoverflies.

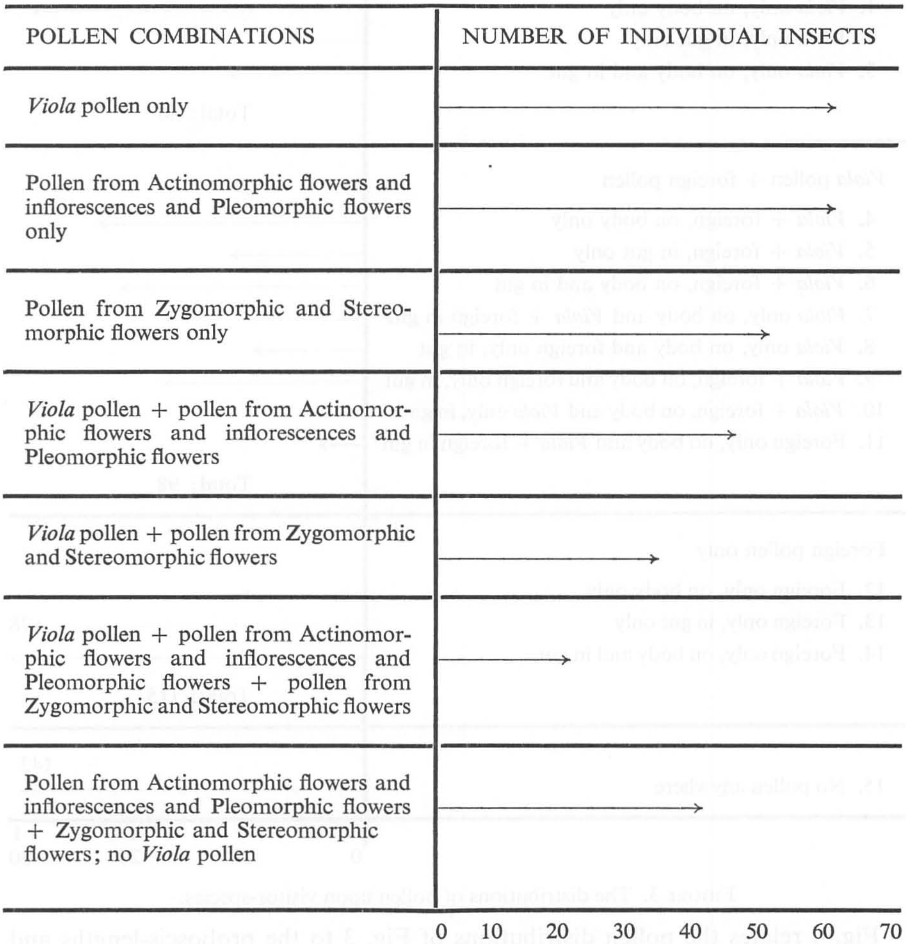

FIGURE 2. The number of individual insects which carried pollen from different flower types.

FOOD SOURCES

Fig. 3 shows the distribution of pollen upon the insects examined. A comparison of categories 1, 4, 8, and 9 with categories 2, 5, and 11 shows that of all the insects which carried *Viola* pollen, the majority carried it on the integument and not in the gut. Analysis of gut contents showed that *Viola* pollen was recorded only 26 times as opposed to 62 times for other pollen species—particularly *Taraxacum*, *Endymion* and *Mercurialis*. These data indicate that, although *Viola* pollen was the food of a variety of visitors, other flowers were the prime pollen source for most anthophilous insects.

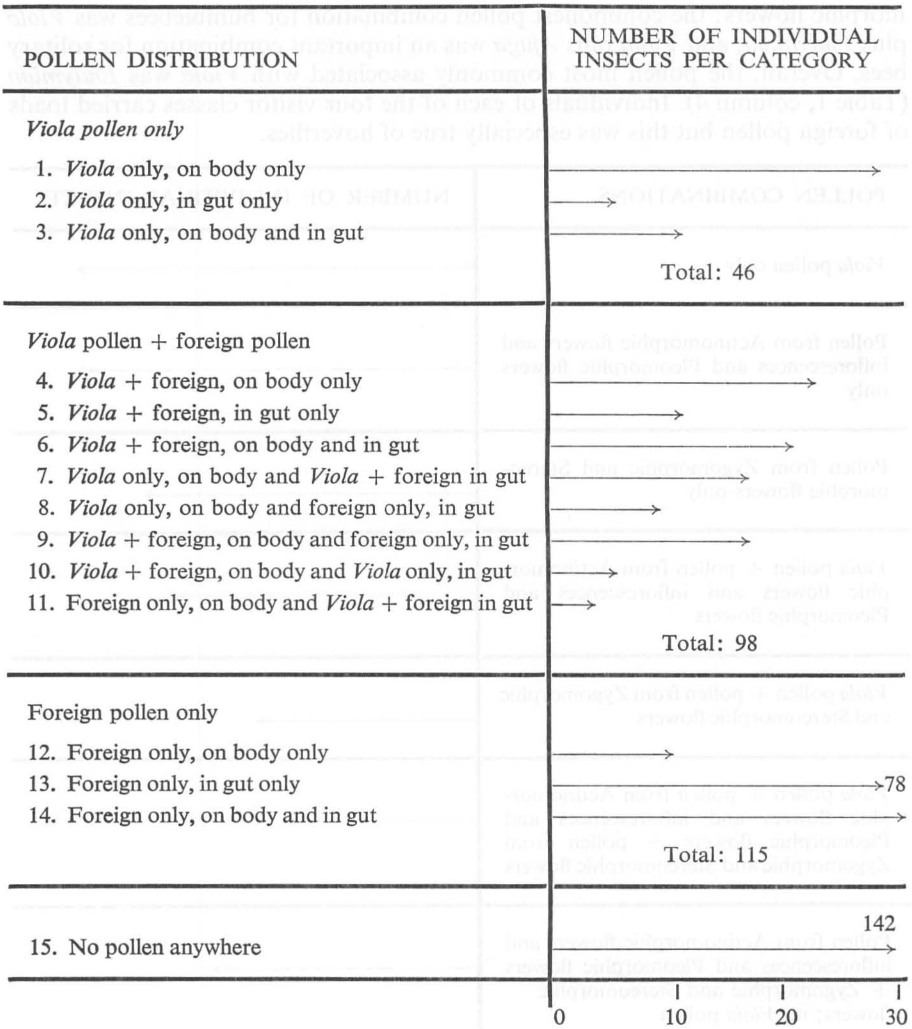

FIGURE 3. The distributions of pollen upon visitor-species.

Fig. 4 relates the pollen distributions of Fig. 3 to the proboscis-lengths and body-lengths of the insects concerned. It shows that the specimens which carried *Viola* pollen on the integument but not in the gut included insects with proboscides of greatly varying lengths. By contrast, the specimens with *Viola* pollen located only in the gut were almost completely confined to the class with the shortest proboscides (1·0–4·0 mm). With regard to body-length, it was clear that most of the insects which carried *Viola* pollen belonged to the class 6·0–11·0 mm. This information collectively suggests that the distribution of *Viola* pollen upon and within insect-visitors is a function both of proboscis and body-length. Proboscis-length seemed to be of particular importance, and influenced the complexity of pollen loads: the majority of individuals which carried a mixture of *Viola* plus foreign pollen belonged to the two classes with the shortest proboscides (1·0–4·0 mm, 5·0–7·0 mm).

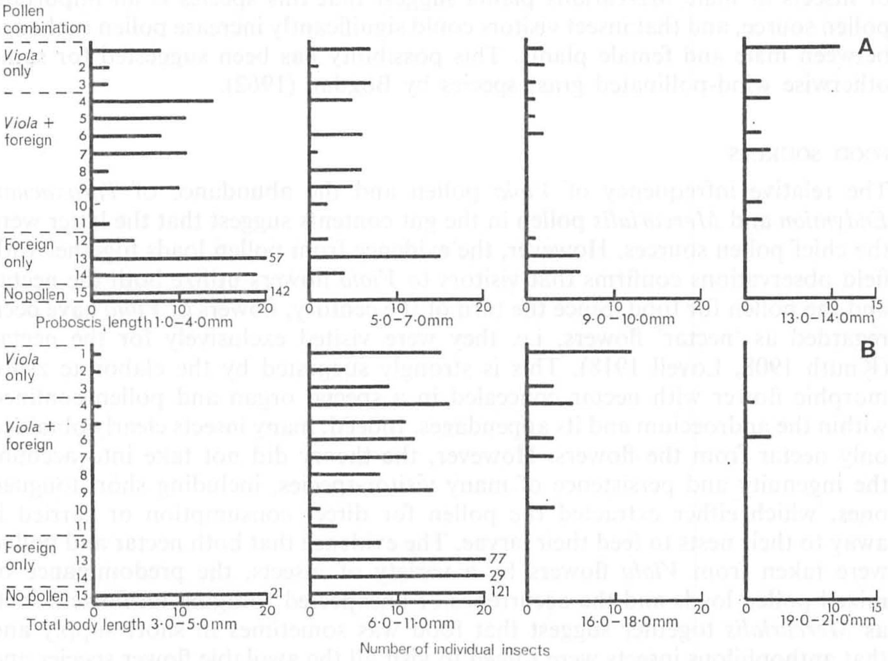

FIGURE 4. Diagrams to show the relationships between the fifteen pollen distributions listed in Fig. 3 and A. proboscis-length, and B. total body-length (but excluding proboscis, antennae or sting).

DISCUSSION

FORAGING

Despite the deliberate selection of habitats with an abundance of *Viola* flowers, the pollen of actinomorphic flowers and inflorescences occurred in pollen loads as many times as that of *Viola*. They were, therefore, at least as important as violets as forage plants for visitor-species. *Taraxacum* was the strongest competitor for *Viola* visitor-species, especially solitary bees and hoverflies. In fact, Graenicher (1935) and Free (1968) have noted that *Taraxacum* is a dominant plant even in the presence of a variety of attractive flowers including highly floriferous fruit trees. On the other hand, the stereomorphic and zygomorphic flowers which were predominantly blue (as opposed to yellow), were clearly the predominant forage plants for social bees; these showed a high preference either for *Viola* or for *Viola* plus one of these types, especially *Endymion*. The data suggest, therefore, some assortative foraging among the *Viola* visitor-species: the solitary bees and hoverflies with a preference for yellow actinomorphs and the social bees with a preference for blue stereo- and zygomorphs.

Mercurialis occupied a rather aberrant position relative to the scheme presented above. Its pollen was commonly found in gut contents and it was clearly an important pollen source. This was of particular interest as *Mercurialis* is generally regarded as wind-pollinated (Clapham, Tutin & Warburg 1962) and yet both honeybees and hoverflies were observed on later occasions combing stands of male *Mercurialis* and collecting or eating the pollen. Frequently their foraging would bring them into contact with female plants. The industry and abundance of insects at male *Mercurialis* plants suggest that this species is an important pollen source, and that insect visitors could significantly increase pollen exchange between male and female plants. This possibility has been suggested for some otherwise wind-pollinated grass species by Bogdan (1962).

FOOD SOURCES

The relative infrequency of *Viola* pollen and the abundance of *Taraxacum*, *Endymion* and *Mercurialis* pollen in the gut contents suggest that the latter were the chief pollen sources. However, the evidence from pollen loads together with field observations confirms that visitors to *Viola* flowers utilize both the nectar and the pollen for food. Since the turn of the century, flowers of *Viola* have been regarded as 'nectar' flowers, i.e. they were visited exclusively for the nectar (Knuth 1908, Lovell 1918). This is strongly suggested by the elaborate zygomorphic flower with nectar concealed in a special organ and pollen confined within the androecium and its appendages. Indeed, many insects clearly obtained only nectar from the flowers. However, the theory did not take into account the ingenuity and persistence of many visitor-species, including short-tongued ones, which either extracted the pollen for direct consumption or carried it away to their nests to feed their larvae. The evidence that both nectar and pollen were taken from *Viola* flowers by a variety of insects, the predominance of mixed pollen loads and the occurrence of unexpected foraging on flowers such as *Mercurialis* together suggest that food was sometimes in short supply and that anthophilous insects were forced to visit all the available flower species and to investigate them persistently in order to get enough to eat. It is probable that *Viola* is a critical pollen source during very early spring when alternatives are in short supply. The dual availability of both nectar and pollen means that the flowers are particularly important resources at this time. Thus, by appearing very early in the season, when competition for pollen vectors may be least, and by harbouring both high-carbohydrate and high-protein food, the chasmogamous flowers receive sufficient insect visits to increase significantly the incidence of cross-pollination. This is an interesting case of ecological factors modifying the situation anticipated by floral biology theory.

CONSTANCY

During March, *Viola* flowers may predominate among the forage plants of many habitats. With the scarcity of alternative food sources many anthophilous insects, which later in the season would feed from less complex flowers, must nevertheless visit *Viola* for food. The result, as the data show (Table 1), is that the foraging of a variety of visitor-species is entirely confined to *Viola*. This behaviour may be termed 'pseudo-constant' since the insects involved have no choice of food.

True flower constancy is well known among anthophilous insects and there appear to be two main types (Linsley & MacSwain 1958). The first is exhibited by individual insects which confine their foraging to one flower species for a limited time. Thus, while many flower species may be exploited during the season, individual insects frequently carry pure pollen loads. The second type is characteristic of whole species or genera of insects and involves physiological, morphological and behavioural adaptations to one or a few species of food plant to which visits are obligatorily confined.

The present study did not reveal any evidence for the second, or obligatory kind of constancy. However, the solitary bees *Osmia*, *Andrena* and *Halictus* and the social bee *Bombus* carried many pure loads of *Viola* pollen. Also, in the field, these insects were observed visiting violets systematically and to the exclusion of other plant species. This evidence indicates that many visits to *Viola* resulted from the first kind of constancy, namely temporary constancy. Species of the four named genera have been shown to exhibit temporary constancy in other situations (Clements & Long 1923, Brittain & Newton 1933, Linsley & MacSwain 1958) and *Osmia biocolor* has been recorded in Germany as having a specific 'predilection' for *Viola* flowers (Schmiedeknecht 1930).

At first, the pure loads of *Viola* pollen carried by hoverflies were thought to result from pseudo-constancy. However, this was not the only cause. *Rhingia campestris* Meigen, when undisturbed, foraged sufficiently slowly to be closely observed. Individuals were seen to visit violets systematically and exclusively. Similar behaviour was noted in *Cheilosia variabilis* Panzer, and in the drone fly *Eristalis pertinax* Scopoli. Twenty-five per cent of *Rhingia* specimens, 20% of *Eristalis* specimens, and 5% of *Platychirus* and *Melanostoma* specimens carried only *Viola* pollen. Knoll (1926) and Ilse (1949), experimenting with possible colour preferences of hoverflies, showed that they responded consistently to some colours and not to others. Minderhoud (1951) discovered that the foraging behaviour of the hoverfly *Eristalomyia tenax* was very similar in many ways to that of honeybees and bumblebees, and Kugler (1970) reported instances of constancy in hoverflies. The possibilities of floral constancy among this insect group has been little explored, however, and this branch of pollination biology requires further study.

Constancy may be important in the pollination of *Viola* in two ways: Firstly, many violets bloom in early spring when food for anthophilous insects may be in short supply. It has been shown that when floral food resources are limited to the flowers of *Viola* the incidence of pollination can be unusually high (Beattie 1968). This may be attributed to the absence of competition with other blossoms for insect visits. On the other hand, when the flowers of a small number of other species are also available the incidence of pollination of *Viola* flowers may be extremely low and, further, the pollen clusters transferred to their stigmatic cavities may be contaminated with foreign types. The contamination of pollen loads lowers the efficiency of the pollination mechanism in *Viola* as foreign grains are ultimately transferred to the stigmatic cavities of the flowers. The style of the flowers of the three *Viola* species under consideration is cylindrical and hollow, its walls enclosing a lumen which is filled with mucilage. The stigmatoid tissue is confined to the walls of the lumen at the distal end of the style and the single point of ingress for pollen grains is a narrow opening at the tip. The opening of the stigmatic cavity is small in relation to the size of the pollen grains and the mechanisms necessary to manoeuvre them through it are fairly precise (Beattie 1971). In addition to this the capacity of most stigmatic cavities is only sufficient to accommodate a number of pollen grains equal to the number of ovules, and a few more. For these reasons pure pollen loads are at a premium as the passage of foreign grains into the stigmatic cavity will reduce the number of ovules fertilized. Constancy among *Viola* visitor-species would increase the frequency of pure pollen loads and so directly affect the number of seeds produced as a result of pollen exchange between chasmogamous flowers.

The second effect of constancy lies in the possibility that this behaviour is exhibited by a cross-section of the visitor-species. The incidence of pollination could be maintained when the visits of one or several of the insect groups failed. This situation may have existed in two of the habitats where violets grew in very small clearings some distance from the edge of the wood. Bees rarely penetrated to this distance (a situation also mentioned by Kerner & Oliver 1895) but on sunny days these spots formed pools of sunlight frequented by hoverflies, especially of the genus *Eristalis* (also noted by Buckton 1895). Pollination of violets in these habitats was almost entirely dependent upon the foraging of hoverflies and would have been most efficient had they been constant to them.

In summary, constancy towards the flowers of *Viola* exhibited by all three groups of pollen vectors will have two important effects: 1. The number of pure pollen loads transferred to the stigmatic cavities will increase thereby ensuring the maximum number of ovules fertilized. 2. The level of pollen exchange between the chasmogamous flowers of the same or of different populations will be increased. Both of these effects may be of special significance in the context of the breeding system as a whole.

Many species of *Viola* are largely in-breeding and develop numerous obligatorily self-pollinated cleistogamous flowers later in the year. In addition to this the capsules produced by these flowers have ineffective dispersal mechanisms for the seeds, which are often dumped very close to the parent plant. The majority of seeds produced by many violet species are derived from these flowers (Valentine 1962, Clausen, Channel & Uzi Nur 1964), consequently large clumps of genetically similar plants are formed; an appropriate strategy for stable environments. On the other hand, cross-pollination of the chasmogamous flowers yields new genetic recombinants which, in conjunction with a more efficient dispersal mechanism, would appear to be most valuable in less stable environments. The combined effects of floral constancy to the chasmogamous flowers is the promotion of cross-pollination and out-breeding in a sexual system otherwise geared to systematic in-breeding.

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